POLYPODIUM VULGARE AS AN EPIPHYTE[1]

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(WITH THREE FIGURES)

While *Polypodium vulgare* is common on rocks, may often grow on the trunks of fallen trees, or sometimes even creep a few feet up living trunks, I have not been able to find a definite report of its being really epiphytic in habit in the United States. SCHIMPER,[2] the first general student of American epiphytes or air plants, says (1888, p. 131):

> In the North American forests the shade plants of the soil would not be able, because of lack of moisture, to grow on the bark of trees. Thus the so common *Polypodium vulgare* ascends to the trees in North America, just as little as it does in central or northern Europe.

Observations made at Cockeysville near Baltimore, Maryland, latitude 39° 30′ N, shows that this polypody can grow and fruit for years as a true epiphyte, high up on the erect branchless trunks of living trees. The ferns were not growing in an unusually moist region, as was true of the epiphytic individuals of it reported by CHRIST[3] (p. 325) as growing near a waterfall as Montreux, or in the damp forests of Portugal (see also SCHIMPER 1888, p. 31). On the contrary, the trees bearing this fern in Maryland were near the top of a northward facing cliff, more than 100 feet above a small stream, and at the western end of a ravine which is about 125 yards wide at this level. Two dozen or more plants of this fern were found growing in the deep furrowed bark of six different chestnut oaks (*Quercus Prinus*). The clumps of polypody were at various heights up to 20 feet or more above the ground. Clumps of all sizes were found, showing that they had started on the tree from prothallia, and had not arisen from rhizomes that had climbed upward from the soil. With one exception they were all on the north side (between N.N.E. and N.N.W.) of single erect trunks.

[1] Botanical contribution from the Johns Hopkins University, no. 70.

[2] SCHIMPER, A. F. W., Die epiphytische vegetation Amerikas. 1888.

[3] CHRIST, H., Geographie der Farne. 1910.

The exceptional case was that of a set of several clumps on a tree which had two trunks from a point about 5 feet above the ground.

FIG. 1.—East side of forked trunk of *Quercus Prinus* (between 2 feet and 6 feet above soil) showing several clumps of *Polypodium vulgare* established as epiphytes on the bark; cards 2×5 inches in size; ×$\frac{1}{8}$.

The two forks of the trunk stood almost in a north and south line, and the crotch between them in an east and west direction. The larger clump of polypody, which bore more than forty full grown leaves, grew just below the fork on the east side of the tree (fig. 1). At 6 inches and at 2 feet below this, on the same side, were two smaller tufts of this fern (fig. 1). Both the latter evidently profited from the collection of considerable water by the fork above, part of which water was directed down the shallow grooves of the bark in which these two clumps grew. This somewhat more abundant water supply, which is likewise more constant, probably explains the presence of these tufts on the east side of the tree, while all the other clumps of this polypody seen were confined to the north sides of the trees. The other five trees on which this fern was growing had trunks that were perfectly straight and without forks or any branches for many feet above the ferns (fig. 3). There was thus no collection of rain, as in the forked trunk, but each clump of polypody was dependent entirely on the portion of water that chanced to run down the particular furrow in which it grew. The fronds of the polypody on the unbranched trunks, although barely half as large as those on the forked trunk, were quite mature, and many of them bore spores. The more favorable growing conditions on the forked tree were indicated not only by the larger size of the polypody itself, but also by the richer growth of bryophytes and lichens, which were much more abundant below the fork than above it on this tree, or than on any of the erect trunks (fig. 2).

Aside from the smaller fronds of the epiphytic polypodies, they apparently were not different from those growing on the soil. In both the rhizome was largely covered by epiphytic liverworts and lichens and sometimes by more or less humus. The external character and internal structure of the rhizome and of the leaf, even to the thickness of the cuticle and of the mesophyll of the latter, were quite alike in plants of both habitats. The roots of both epiphytic and terrestrial plants were abundant, closely matted, and thickly beset with root hairs. Many of these root hairs had one or more fungous hyphae running lengthwise through them. These hyphae could often be seen entering at the tips of the root hairs. Whether they have the function of mycorhizal fungi has not been determined.

FOOD OF EPIPHYTES.—Not only the water, which was running over the bark of the supporting tree, but also the indispensable mineral foods dissolved in it, are absorbed by the roots of the epiphytic fern. In the locality under discussion, as well as in the wet tropical forests where epiphytes are most abundant, there can be but minute traces of mineral dust from the forest covered soil

FIG. 2.—Several clumps of polypody from near x in fig. 1, showing epiphytic lichens and liverworts, fruiting fronds of fern above, and young plants developed from prothallia below x at left; $\times\frac{2}{3}$.

blown by winds to the tree tops, to be washed down over the trunks by rains. It is evident, therefore, that the air plant is really dependent on the tree not only for support, in an advantageous position for light, but it must also rely on the tree to raise from the soil the food salts needed. In other words, the mineral-containing substances, resulting from the disintegration of bark, twigs, and leaves of the supporting tree (or perhaps a neighboring one), and

which are then washed down to the epiphyte, must first be carried above the epiphyte by the water vessels inside the tree. The epiphyte is to this extent dependent on a physiological process of the living host, the upward conduction of water, which involves a considerable expenditure of energy. The mineral food demands made upon the tree by the epiphyte are thus somewhat equivalent to those made by the "half-parasite" of its host. The chief difference is that the mistletoe exacts its quota of salts (and of water also) from within the living host, before they have been

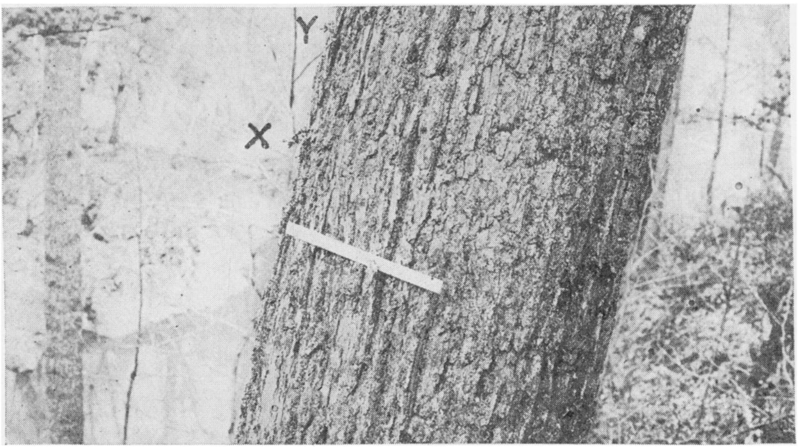

FIG. 3.—Trunk of *Quercus Prinus* bearing at x and y (north side of tree) two tufts of *Polypodium vulgare;* upper tuft 9 feet above soil, others above this are 18 or 20 feet from ground; $\times\frac{1}{15}$.

used by the host itself, while the air plant gets its salts from the surface of the tree after they have served their function within it. The water obtained by the epiphyte of course has never been inside the supporting tree. If the mistletoe is to be called a "water (and salts) parasite," the epiphyte is a "salts saprophyte"; that is, it secures its mineral food from the dead and no longer functional portion of the supporting plant.

ORIGIN OF TEMPERATE ZONE EPIPHYTES.—SCHIMPER (1888) announced the very important generalization that the vast majority of all vascular epiphytes are of tropical origin. Of extratropical epiphytes he believed that only the relatively few types found in

the rain forests of southern Chile and of New Zealand, with perhaps a couple of epiphyte ferns in Japan and southern Australia, are indigenous in origin. The other temperate zone epiphytes of the Old World, of South America, and according to SCHIMPER all epiphytes of temperate North America, have acquired this habit while in the tropical forest. SCHIMPER stated that it is the most xerophytic of the tropical epiphytes, those growing on the branches of the relatively dry roof of the forest, that have wandered out across the neighboring savannas and subtropical forest and onward sometimes 10 or 15 degrees beyond the tropics to populate with epiphytes the warmer and moister of the neighboring temperate forests. Because of the adaptation of these epiphytes to the dry conditions at the top of the forest, they have been able, in spite of the still more rigorous conditions encountered there, to colonize certain temperate forests. For the epiphyte that migrates from the tropics to the temperate zone, probably the most critical adverse condition encountered is not the occasional hot, dry summer, but the periods of low humidity during the generally wet winter season, when cold, dry, northwesterly winds prevail, during which the evaporation rate is high and water cannot be absorbed by the frozen roots. For example, the writer has noticed that tufts of *Tillandsia usneoides*, hung on a deciduous magnolia tree each year in May, thrive and grow rapidly during the summer, and even look fresh and green after several frosts in the autumn. They ultimately succumb, however, to the cold dry westerlies of winter, even of so moderate a winter as that of 1920–21. The precise measurement of the evaporating power of the air at these low temperatures, a factor of prime importance also to terrestrial plants, especially evergreen ones, must await the invention of a practicable frost-proof evaporimeter. Possibly the exposure of the epiphyte to sunlight, when the supporting tree is bare of leaves, is directly injurious also, although this seems hardly likely, since this same *Tillandsia* is abundant on deciduous trees only 200 miles south of Baltimore, where the winter sunlight would probably be at least as strong. The sunlight of course must work harm indirectly by increasing transpiration, which probably explains the usual restriction of polypody to the north sides of the trees.

The epiphytic ferns and seed plants of temperate North America, such as *Polypodium polypodioides*, *P. aureum*, *Vittaria lineata*, *Psilotum triquetrum* Sw. (=*P. nudum* [L.] Griseb.), *Tillandsia usneoides*, and *Epidendrum conopseum*, and the eighteen others named by SCHIMPER, have each a more or less widespread distribution in the American tropics, from whence they have probably migrated northward. The occurrence of *Polypodium vulgare* as an epiphyte in temperate North America, therefore, has a very interesting bearing on this question of the possible origin of extra-tropical epiphytes. For this fern, although distributed across the whole north temperate zone, in the New World from western Canada to Maine and south to Missouri and Georgia, and from Great Britain to Japan and southward into Northern Africa, is not known in the tropics, neither have fossils of it as yet been found there. We have no adequate evidence, therefore, that *Polypodium vulgare* acquired in the tropics the epiphytic habit which it assumes occasionally in Maryland, and more frequently in the damp forests of Portugal and Azores (SCHIMPER, 1888; CHRIST, 1910). The occurrence of this fern (or a closely similar polypody) in Cape Colony suggests that it may have crossed the equator by land, but of this there is no positive evidence, and this view seems negatived by the lack of fossils in equatorial Africa, and also by the absence of this polypody at the present day from the temperate highlands of the eastern tropics. From what is known of the habitats of *Polypodium vulgare* it seems most probable that this species is primarily a terrestrial plant of temperate forests. It probably entered North America from Eurasia via Alaska, and thence spread southward and eastward. It has acquired great hardiness while living on dry rocky ledges, often with a very scant water supply, and with no more soil than can collect in a few minute cracks of the rock. Thus this temperate zone polypody has come to be able to persist also in some shaded situations, on the very precarious supply of water and minerals to be found on the trunk of a rough barked tree. This is clearly true in spite of SCHIMPER's somewhat too positive statement (1888, p. 152) that "in the less damp North American forests the first step, the migration of the terrestrial plants to the trees, is impossible, and herewith the origin

of an indigenous epiphytic association is excluded from the beginning." This *Polypodium* seems evidently an endemic epiphyte of the temperate zone, and not one imported with this habit already formed from the tropics. It might well be designated a facultative epiphyte. In its ability to live on various substrata it closely resembles dozens of species of ferns and seed plants of the tropical forests which can be found growing, now on soil, now on dry rocks, and again as epiphytes on tree trunks.

It might perhaps be suggested that more of our temperate zone plants should prove able to live on trees. As a matter of fact, however, few of our saxicolous vascular plants are really as hardy as this polypody, the thick-cuticled leaves of which are capable of rolling up in dry weather and so of lessening transpiration. The combination of these two features, uncommon in plants of this region but common in epiphytic ferns of the tropics, is probably an important one in enabling this fern, and likewise its relative *Polypodium polypodioides*, to adopt the epiphytic habit. The evergreen leaves of *Polypodium vulgare*, which are also characteristic of most, although not of all epiphytes, are probably of great importance to this plant of shady deciduous forests. They enable it to carry on an important share of its photosynthetic work on any mild days between October and May, when abundant light reaches it because the surrounding trees are bare of leaves. In other words, while growing on soil or rocks this fern has developed more of these xerophytic characters, which fit it for living as an epiphyte, than perhaps any other vascular plant of the northeastern United States. It seems at the present time to be an indigenous temperate-zone epiphyte in the making.

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